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# Reduced herbivory during simulated ENSO rainy events increases native herbaceous plants in semiarid Chile

Rosa Manrique · Julio R. Gutiérrez ·  
Milena Holmgren · Francisco A. Squeo

**Abstract** El Niño Southern Oscillation (ENSO) events have profound consequences for the dynamics of terrestrial ecosystems. Since increased climate variability is expected to favour the invasive success of exotic species, we conducted a field experiment to study the effects that simulated rainy ENSO events in combination with herbivores and shade have on the composition of a semiarid herbaceous community in north-central Chile. We hypothesized that water pulses, such as those associated with rainy ENSO events could trigger significant changes in the relative abundance of exotic and native herbaceous species. Specifically, we predicted an increase in native grasses and a reduction in the abundance of exotic species,

especially prostrate forbs, if water pulses were combined with reduced herbivory. We found that herbivory by small mammals, especially introduced European rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*), have an overwhelming effect on species abundance and composition in this semiarid herbaceous community. Herbivore exclusion produced an overall increase in herb density and biomass mostly due to the extraordinary growth of tall native grasses (especially *Bromus berterianus*) that outcompeted small prostrate forbs (both native and exotic ones), and small exotic grasses (*Koeleria pleoides*, *Schismus arabicus*). Our results suggest that it might be possible to enhance the recovery of native grasses by applying efficient herbivore control during rainy years such as those associated with ENSO events although a negative consequence would be the loss of small native forbs, which greatly contribute to the richness of herbaceous communities in semiarid ecosystems.

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R. Manrique · J. R. Gutiérrez (✉) · F. A. Squeo  
Departamento de Biología, Universidad de La  
Serena, Casilla 599, La Serena, Chile  
e-mail: jgutierrez@userena.cl

J. R. Gutiérrez · F. A. Squeo  
Centro de Estudios Avanzados en Zonas  
Áridas—CEAZA, La Serena, Chile

J. R. Gutiérrez · F. A. Squeo  
Instituto de Ecología y Biodiversidad, Universidad de  
Chile, Casilla 653, Santiago, Chile

M. Holmgren  
Resource Ecology Group, Wageningen University,  
Bornsesteeg 69, Building 119, 6708 PD Wageningen,  
The Netherlands

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## Introduction

El Niño Southern Oscillation (ENSO) is a recurrent oscillation (typically once every 3–6 years)

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that alters the oceanic and atmospheric patterns in large regions around the world. During an El Niño episode, rainfall dramatically increases in certain areas of the world reaching 4–10 times that of a “normal” year. The phenomenon lasts approximately 1 year until climate conditions reverse (Allan et al. 1996). Despite the great uncertainty about the effects of global climate warming on ENSO dynamics (Collins 2000), recent high resolution climatic models suggest that the frequency of El Niño-like conditions could increase during the coming decades (Timmermann et al. 1999). In fact, El Niño events have increased in frequency in the last decades (Trenberth and Hoar 1997; Tudhope et al. 2001).

ENSO events have major consequences for the dynamics of terrestrial ecosystems (Holmgren et al. 2001, 2006; Stenseth et al. 2002). In arid and semiarid ecosystems, rainy ENSO years cause an extraordinary increase in primary productivity that cascades upwards to higher trophic levels (e.g., Meserve et al. 2003). Herbaceous communities respond most spectacularly through the massive germination of annuals and the growth of perennial herbs (e.g., Dillon and Rundel 1990; Gutiérrez et al. 1997, 2000; Polis et al. 1997).

These rainy pulses could have strong effects on the composition of herbaceous communities by for instance favouring the dominance of species with higher growth rates in response to increased water availability. However, changes in plant abundance often result from interactions between several environmental factors. For example, in a large-scale field experiment following the responses of a semiarid north-central Chilean scrub community to rainy ENSO events, the cover of herbaceous plants, especially exotic annuals, decreased when small rodents were excluded. Apparently, small rodents reduce shrub cover by browsing and increase soil disturbance which facilitates the colonization of disturbed patches by annuals (Gutiérrez et al. 1997). In northern Peru, rainy ENSO events have an indirect effect on plant invasion by favouring the incidence of fires which trigger an extraordinary abundance of exotic herbs in burnt stands (Block and Richter 2000). Obviously, ENSO-induced changes in plant communities could further expand by competitive effects (i.e., if a species effectively reduces

resources available to others) or through ecosystem changes (i.e., if the increase in a species alters ecosystem dynamics such as the disturbance regime or nutrient cycling).

In contrast to results showing an increase in the proportion of exotic species during high water availability pulses (see also Hobbs and Mooney 1991; Milchunas and Lauenroth 1995; Daehler 2003), we hypothesize that rainy ENSO events could potentially increase the abundance of native herbaceous species under certain circumstances. If rainy ENSO events favoured an increase in the abundance of native tall grasses, these in turn would likely be able to outcompete shorter, prostrate species. The overall community effects would largely depend on the initial relative abundance of prostrate and erect lifeforms among native and introduced species. A community formed predominantly by native grasses could reduce the invasibility success of exotic species, especially prostrate forms during ENSO events by rapidly increasing in abundance and outcompeting exotic species. Alternatively, a community formed mainly by prostrate native species could be more easily invaded by exotic grasses. We predict that the interaction between the rainy ENSO pulses and other environmental factors, particularly herbivory and shade, would be crucial. If native grasses are more susceptible than exotic grasses to herbivores, then an increase in native species can only be expected if herbivores are reduced. Since herbivores respond positively to increases in primary productivity during rainy ENSO events (e.g., Meserve et al. 2003), herbivory is expected to play a major interactive role with rainfall in explaining changes in the relative abundance of native and exotic species.

Exotic grasses and forbs have successfully invaded the scrub and shrublands of north-central Chile (Gulmon 1977; Groves 1986; Montenegro et al. 1991; Arroyo et al. 1995; Squeo et al. 2001; Figueroa et al. 2004) in a process strongly influenced by introduced grazers (Fuentes et al. 1984, Jaksic and Fuentes 1991; Holmgren 2002). In this paper, we present the results of a field experiment to study the interaction between experimentally simulated rainy ENSO conditions, shade, and small mammal herbivores on a semiarid herbaceous community in north-central Chile. We

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address the following questions: (1) Do exotic species increase in abundance during experimental high water availability pulses? (2) How does the interaction between increased water availability, herbivory exclusion and shade affect the abundance of exotic species?

### Study site

The study site was located within a private farm (Fundo El Salitre) next to the Parque Nacional Bosque Fray Jorge, 85 km south of La Serena (30°41' S, 71°37' W), in north-central Chile. This old field has a south-east orientation on a gentle slope (10°, 200 m a.s.l) and is currently being used for livestock grazing. The climate is semiarid mediterranean with 90% of the precipitation in the winter months (May–September); summer months are warm and dry. Mean annual precipitation is  $145.4 \pm 31.3$  mm (1 SE) (1989–2002, Fray Jorge weather station). In ENSO years, annual precipitation reaches around 200 mm while in La Niña years it decreases to less than 50 mm. The accumulated rainfall in 2002, when the study was carried out, was 337.2 mm which was three-fold higher than the average, as a result of a moderate ENSO event (Aceituno 2002; McPhaden 2004). The vegetation is dominated by xerophytic shrubs such as: *Gutierrezia resinosa*, *Proustia cunneifolia*, *Senna cumingii*, *Bahia ambrosioides*, *Flourensia thurifera*, *Baccharis* sp., *Heliotropium stenophyllum*, *Haplopappus foliosus* and the cactus *Echinopsis skottsbergii*.

## Methods

### Experimental design

We designed a factorial experiment with three factors (water, herbivory, and shade). Each factor had two levels, resulting in eight treatments ( $2 \times 2 \times 2$ ). Each treatment was replicated in five blocks. Treatments were arranged in a split-block experimental design, with water being the whole unit, and herbivory and shade the sub-units. Each block consisted of eight experimental plots of  $6 \times 6$  m. Each block was divided into two groups of four plots. We first randomly assigned the

water treatment to each group. We then randomly assigned the combination of herbivory and shade treatments within each water treatment group. In order to avoid uncontrolled run-off water effects, we installed metal plates to a depth of 20 cm around each plot leaving a strip of 5 cm above ground.

Water treatments were: watered (natural rainfall plus 150 mm extra irrigation to simulate an average El Niño year) and no watered (only natural rainfall). However, due to heavy natural rainfall, our actual water treatments simulated conditions of strong to very strong rainy years: watered (337 mm natural rainfall plus 150 mm extra water) and unwatered (337.2 mm natural rainfall). Water was collected from a nearby river (Limarí River) and transported in a water container to the experimental site. The water was transferred to two water tanks (5,500 l each) in the field and pumped from there through PVC piping to the experimental plots. To simulate natural rainfall, we sprinkled water through nine micro-jects per plot (located at 2-m intervals and 1 m high). Irrigation was done once in June (40 mm), July (40 mm), August (40 mm) and September (30 mm) 2002, following the natural rainfall seasonal pattern described for this region (López-Cortes and López 2004).

Herbivory treatments were: presence (open-access plots) and absence (closed-access plots) of small mammal herbivores. All large herbivores (such as domestic livestock) were excluded using a 800 m-perimeter fence around the whole experiment setting. The fence allowed the free transit of all small mammals such as rodents, rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*). To exclude these small herbivores from the experimental plots, we used 2-m high galvanized fences (0.5 cm mesh), buried 30 cm into the ground and with 25 cm strip flashing at the upper part of the fence.

Shade treatments were: shaded and unshaded. Shading black nets (50% irradiance reduction) were placed 1.5 m high over the experimental plots and additional netting on the sides to avoid lateral light infiltration. This shaded condition simulates the irradiance levels found under the cover of natural shrubs (F.A. Squeo, unpublished results). We removed the aboveground biomass

of all woody shrubs from the plots to avoid uncontrolled effects of competition, shade or water hydraulic lift (Squeo et al. 1999).

### Plant sampling

In each experimental plot (6 m × 6 m), four (30 cm × 30 cm) fixed quadrats were randomly installed (i.e., a total of 160 quadrats). In each quadrat, we counted all plants at monthly intervals during the growing season of 2002 (May–November). We also estimated plant biomass at the peak of the growing season (October) since plant species may respond to microhabitat conditions either by establishing more but smaller individuals or by growing fewer but larger ones. We harvested all plants inside four randomly selected 30 cm × 30 cm quadrats per plot. Plant material was oven-dried at 70°C until constant dry weight was reached, and average biomass expressed as weight per area unit (Brower et al. 1989).

### Statistical analysis

We used repeated measures analysis of variance to estimate treatment effects on plant density and richness taking into account the block split plot experimental design for the error terms (Zar 1999). Biomass data were analysed through a factorial analysis of variance. Both density and plant biomass were  $\ln(x + 1)$  transformed prior to statistical analyses because of the large variances. All *P*-values were Huynh-Feldt-adjusted, a procedure that corrects for deviation in the sphericity assumption of the variance co-variance matrix (von Ende 1993). We made planned comparisons sorting the data in the following categories: all annual species, and species pooled by life-form (forb or grass) and origin (exotic or native).

## Results

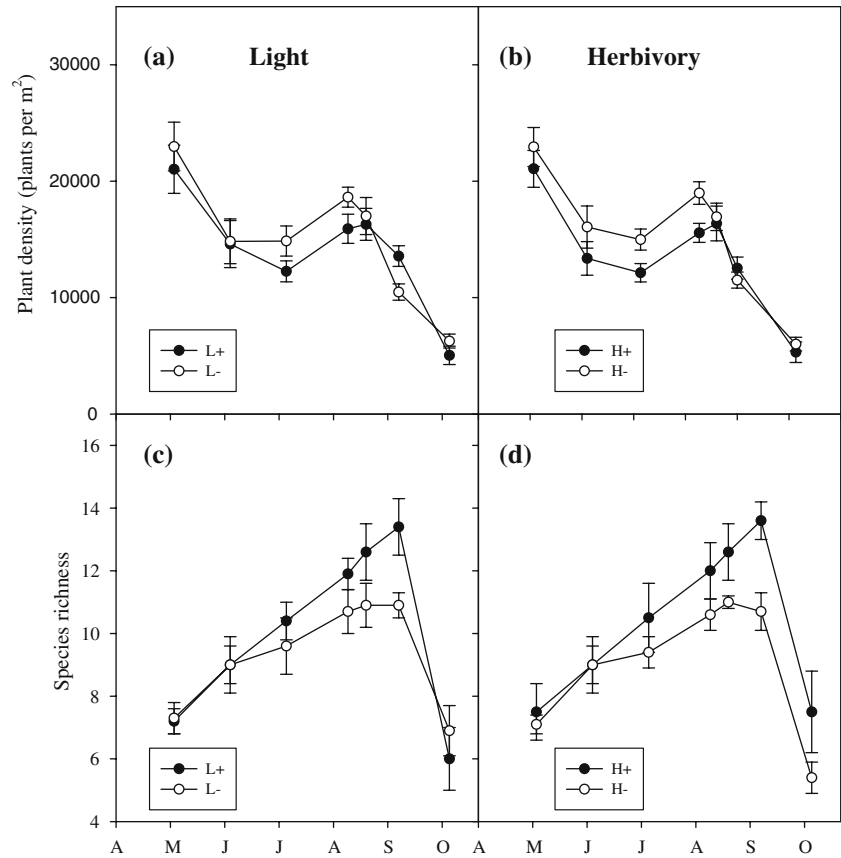
### Plant density and species richness

Total plant density (all species pooled) was not significantly different between the two water

treatments; however, through time, it was significantly higher in shaded plots ( $F_{(6,192)} = 5.02$ ;  $P < 0.001$ ) and closed-access plots ( $F_{(6,192)} = 2.60$ ;  $P = 0.027$ ) (Fig. 1a, b). Species richness through time showed the opposite pattern, namely a reduction in shaded plots ( $F_{(6,192)} = 3.14$ ;  $P = 0.006$ ), and closed-access plots ( $F_{(6,192)} = 2.31$ ;  $P = 0.036$ ) (Fig. 1c, d). There was lower richness in shaded and closed-access plots where native grasses reached their highest biomass.

Forb (prostrate plants, 1–5 cm tall) species were the main source of species richness. Density of native forbs was higher in unwatered (Fig. 2a;  $F_{(6,192)} = 2.57$ ;  $P = 0.0234$ ), unshaded (Fig. 2c;  $F_{(6,192)} = 3.79$ ;  $P = 0.0036$ ) and open-access plots (Fig. 2e;  $F_{(6,192)} = 2.52$ ;  $P = 0.0354$ ) through time. Native forb density was always higher in grazed than ungrazed treatments independently of the water and shade availabilities (Fig. 3a, b). Neither the interaction water × herbivory nor the interaction shade × herbivory treatments were significant for native forbs ( $F_{(1,24)} = 0.21$ , 0.94;  $P = 0.6534$ , 0.3429; respectively). The most abundant native forbs were: *Adesmia tenella*, *Plagiobothrys collinus*, *Chaetanthera linearis*, *Eryngium coquimbannun*, *Lastarriaea chilensis*, *Pectocarya dimorpha*, and *Plantago hispidula*. As for native forbs, density of exotic forbs was also higher in the unwatered plots (Fig. 2b;  $F_{(6,192)} = 2.59$ ;  $P = 0.0286$ ) and in the unshaded plots (Fig. 2d;  $F_{(6,192)} = 2.76$ ;  $P = 0.0210$ ) through time, but it did not show a significant response to the herbivory treatment (Fig. 2f;  $F_{(6,192)} = 1.74$ ;  $P = 0.1292$ ). Native forbs responded more strongly than exotic forbs to the experimental treatments, particularly water and herbivory (Fig. 2). For example, density of native forbs (based on an average value for the whole growing season) was 177% higher in the unwatered compared to watered plots, versus 31% for exotic ones. Similarly, density of native forbs was 125% higher in the open-access plots compared to closed-access plots, while only 11% for exotic forbs. The response to light condition is also noteworthy; density of native forbs was 48% higher under full-light condition compared to shaded plots and only 7% for exotic ones. Neither

**Fig. 1** Plant density (all species pooled) and species richness responses to light (L) and herbivory (H) in north-central Chile during 2002. Light treatments: L+, full natural irradiance; L-, 50% irradiance reduction. Herbivore treatments: H+, open-access plots to herbivores; H-, closed-access plots to herbivores. Error bars are 1 SE



native nor exotic grass density responded significantly to the treatments.

### Biomass

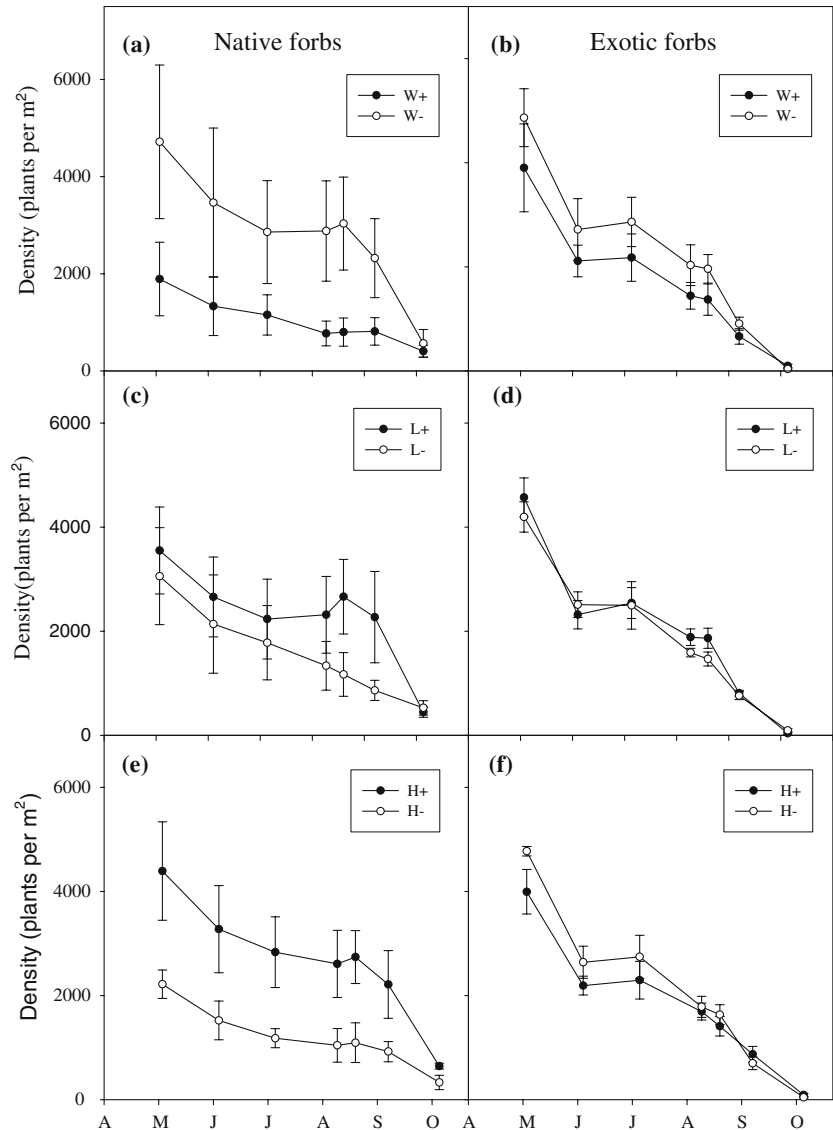
As with plant density, total plant biomass (all species pooled) did not show a significant response to the water treatments, but it was significantly higher in shaded ( $F_{(1,24)} = 4.89$ ;  $P = 0.037$ ) and closed-access plots ( $F_{(1,24)} = 5.75$ ;  $P = 0.025$ ). Native grasses had the highest biomass in the shaded and closed-access plots (Fig. 4;  $F_{(1,24)} = 6.44$ ;  $P = 0.018$ ). When herbivores were excluded, native grasses increased three-fold in abundance in shaded plots, reaching 35% more biomass than exotic grasses. The most abundant native grass was the 10–20 cm tall *Bromus berterianus* ( $66.34 \pm 12.05$  g/m<sup>2</sup>, Fig. 4) which followed a similar biomass pattern response with respect to herbivore  $\times$  shade treatment ( $F_{(1,24)} = 6.62$ ;  $P < 0.015$ ). Exotic

grasses did not show any significant response to the experimental treatments. These results indicate that native grasses are more sensitive to the presence of herbivores than exotic grasses. In contrast, biomass of native forbs was more than twice as high in the unwatered plots ( $F_{(1,4)} = 16.12$ ;  $P = 0.0159$ ) as it was in the watered ones (Fig. 5). Biomass of native forbs did not show any significant response to the shade and herbivore treatments. Biomass of exotic forbs did not show any significant response to the experimental treatments.

### Discussion

We hypothesized that water pulses, such as those associated with rainy ENSO events could trigger significant changes in the relative abundance of exotic and native herbaceous species. Specifically, we predicted an increase in native grasses and a

**Fig. 2** Density responses of native and exotic forbs to water (W), light (L), and herbivores (H) in north-central Chile during 2002. Water treatments: W+, irrigated plots simulating a very strong ENSO event; W-, unwatered plots simulating a moderate ENSO event. Herbivore treatments: H+, open-access plots to herbivores; H-, closed-access plots to herbivores. Light treatments: L+, full natural irradiance; L-, 50%-irradiance reduction. Data are mean  $\pm$  1 SE

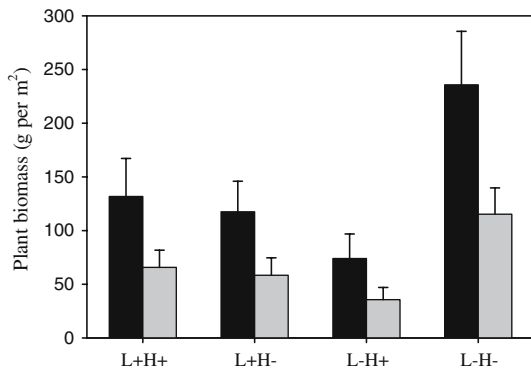
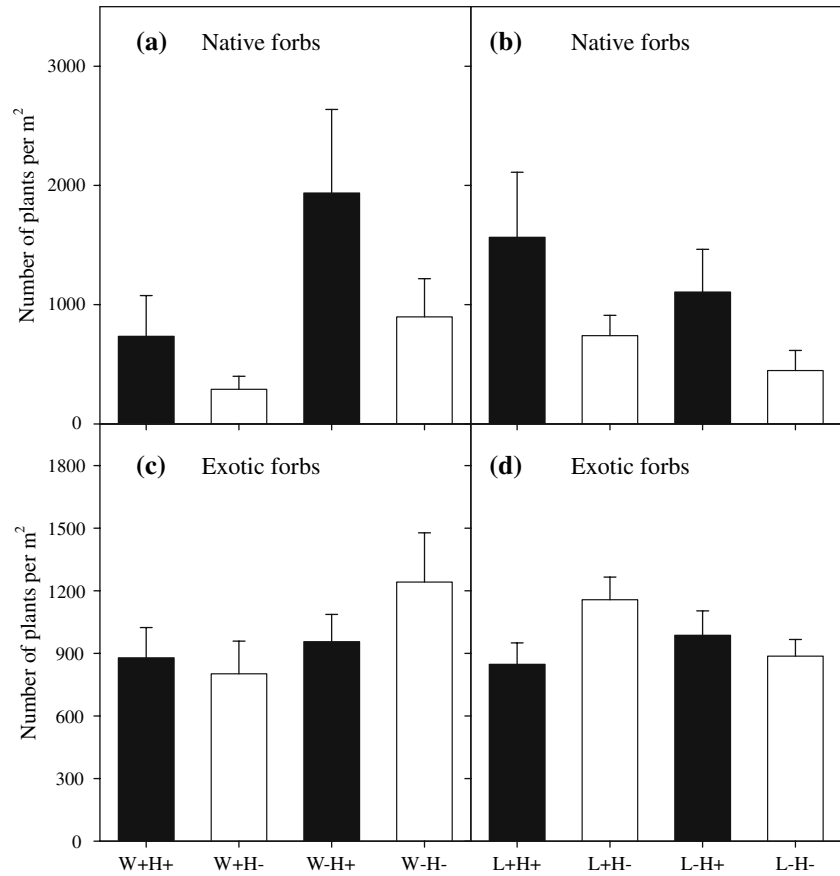


reduction in the abundance of exotic species, especially prostrate forbs, if water pulses were combined with reduced herbivory. The field experiment was conducted in 2002, which was coincident with a moderate ENSO event (Aceituno 2002; McPhaden 2004). This means that the two water treatments were equivalent to a moderate ENSO event (337 mm of natural rainfall), and a mega rainy year (337 mm natural rainfall plus 150 mm irrigation). Indeed the highest precipitation recorded for the region has been 478 mm during the ENSO of 1905 (period

1900–2003), which is close to the 487 mm precipitation of our wettest experimental treatment.

Although massive germination of annuals is among the most spectacular effects of rainy ENSO events on plant communities (Gutiérrez et al. 1997; Polis et al. 1997), our experimental results show that herb growth was not significantly different when comparing water conditions that simulate moderate versus very strong ENSO events. Moreover, the abundance of prostrate forbs (both native as exotic) actually declined at extremely wet conditions. Our results indicate a

**Fig. 3** Density responses of native and exotic forbs to grazing under different conditions of water and light availability in north-central Chile. Data are average density during the growing season in 2002. Symbols as in Fig. 2. Error bars are 1 SE



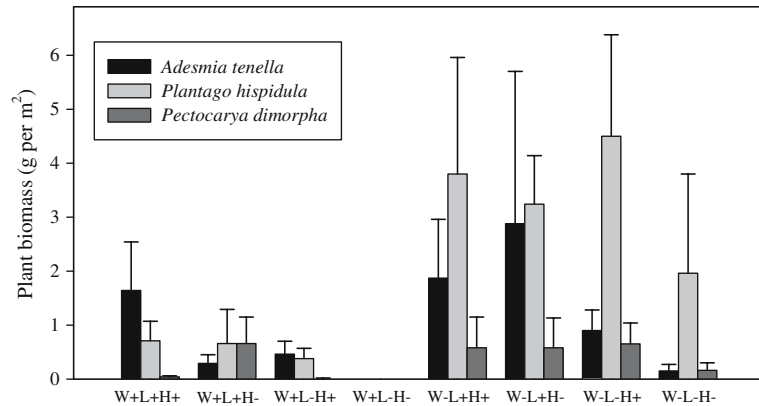
**Fig. 4** Biomass response of native grasses (black bars) and *Bromus berterianus* (gray bars) to the light  $\times$  herbivory treatment in north-central Chile. Symbols as in Fig. 1. Error bars are 1 SE

saturation response of the herbaceous species to very wet conditions. This negative response of forbs to extreme wet conditions contrasts with results described for Californian grasslands where

native forbs actually increased dramatically during very strong rainy ENSO years (Seabloom et al. 2003).

We found that herbivory by small mammals, especially introduced European rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*), had an overwhelming effect on the abundance and richness of plants in these semiarid herbaceous communities. As expected, herb density and biomass were more abundant in protected plots; however, not all species responded in a similar way. Herbivore exclusion increased the abundance of principally tall native grasses (especially *Bromus berterianus*), and reduced the abundance of small prostrate forbs (both native and exotic ones), and small exotic grasses (*Koeleria pleoides*, *Schismus arabicus*). Rabbits and hares were introduced about a century ago and have proven to be extremely damaging to native herbs and shrubs (Jaksic and Fuentes 1991; Holmgren 2002).

**Fig. 5** Biomass response of native forbs to the water, light and herbivory treatment in north-central Chile. Symbols as in Fig. 2. Error bars are 1 SE



Favoured by a lack of predators, rabbits and hares move freely in open spaces feeding preferentially on native shrub seedlings (Fuentes et al. 1983, 1984) and herbs (Jaksic and Fuentes 1980). Native grasses seem more susceptible to grazing than exotic grasses. In our experiment, native grasses increased about three times in abundance when herbivores were excluded whereas exotic grasses did not respond to the treatments. In a comparable herbivore-exclusion experiment performed with herbs of the Chilean matorral (native evergreen shrublands found to the south in central Chile), grazing by rabbits and hares had also stronger effects on native grasses (*Bromus berterianus*) than exotic grasses (*Lophocloa cristata*) (Holmgren et al. 2000). In the matorral, grazing by these introduced herbivores reduced the abundance of grasses and facilitated the dominance of mainly exotic forbs (e.g., *Erodium cicutarium*) (Holmgren et al. 2000). The dominance of forbs at increasingly grazed sites has been observed in other Mediterranean ecosystems as well (e.g., Noy-Meir et al. 1989). In our experiments, forbs likely declined due to the reduction in light availability produced under the dense cover of erect native grasses that grew when herbivores were excluded. Indeed our experiments show that forbs become less abundant in both shaded plots as well as in closed-access plots. The response of forbs to grazing will likely depend on the overall water conditions. Research in mesic grasslands has shown that grazing can strongly increase the abundance and richness of annual forbs by increasing light

availability through either reducing grass height (Hayes and Holl 2003) or cover (Tilman 1993). In contrast, research in more xeric grasslands suggests that grazing decreases the cover of forbs (Waser and Price 1981) by eliminating plants that provide shade and ameliorate water stress (Watt and Gibson 1988). In our experiments which simulated strong to very strong rainy conditions in semiarid communities, we found that the abundance of forbs was always higher under the grazed treatments. Our results show that under extremely wet conditions, semiarid herb communities respond in a comparable way to mesic grasslands (Tilman 1993; Hayes and Holl 2003).

It is noteworthy that the increase in biomass of native grasses when herbivores are excluded is restricted to shaded plots. We can only speculate on the mechanisms behind this strong interaction effect. It could be that at full sun conditions, grasses are facing growth limitation by other factors, for instance, water stress, overheating and/or photoinhibition. All of these factors could affect their photosynthesis rate directly, and impede biomass production even when herbivores are excluded. Alternatively, it may well be that improved grass growth under shaded conditions (perhaps partly due to improved water relations) attracts herbivores towards those plots and therefore, their effect is stronger there. Finally, both mechanisms could be playing a role simultaneously.

Herbivore exclusion and shade produced comparable patterns, namely an increase in plant density at the cost of a reduced species



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richness. In a shaded environment with no herbivores, herb biomass reached the highest levels due to the extraordinary growth of the tall native grass *Bromus berterianus*. This inverse relationship between biomass and species richness (Rosenzweig 1987) in years of high productivity (rainy conditions) may result because the dominant species (e.g., *Bromus berterianus*) is better able to monopolize the available resources (i.e., space, nutrients) increasing its biomass at the expense of inferior competitors (Pyke and Archer 1991) such as prostrate forbs and shorter grasses. Our results show that under water conditions comparable to moderate and strong rainy years, herbivore exclusion and shade can favour the growth of native grasses and decrease the abundance of exotic plants. Comparable patterns have been observed in a long-term and large-scale field experiment installed very close to our experimental site (Gutiérrez et al. 1997). This general pattern of a strong increase in the abundance of native grasses when herbivores are excluded and an associated decline in species richness through a strong reduction in exotic species has been found in several semiarid grassland systems (e.g., McNaughton 1979; Sala et al. 1986). Note that in our experiments the increase of native grasses not only reduced the abundance of exotic prostrate forbs but also decreased the density of native forbs which contribute greatly to species richness. Native forbs were more abundant in unshaded and open-access plots.

Our data support the hypothesis that water pulses such as those associated with rainy events can trigger significant changes in the composition of semiarid herbaceous communities due to interacting effects among water, shade and herbivory. But our results also suggest that, in contrast to what has been found in many previous studies, increased water availability can produce an increase in native plants that reduces the success of exotic plants. Although increased rainfall can initially stimulate the growth of both native and exotic herbs, herbivore exclusion and shade favour erect native grasses which in turn can outcompete small prostrate species. Our results suggest that it

might be possible to enhance the recovery of native grasses by applying efficient herbivore control during rainy years such as those associated with ENSO events but a negative consequence would be the loss of small native forbs which greatly contribute to the richness of herbaceous communities in semiarid ecosystems.

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## References

- Aceituno P (2002) Boletín Climático. Departamento de Geofísica. Universidad de Chile ([http://met.dgf.uchile.cl/clima/HTML/BOL\\_ANT/SEPTIEMBRE02/septiembre02.htm](http://met.dgf.uchile.cl/clima/HTML/BOL_ANT/SEPTIEMBRE02/septiembre02.htm))
- Allan R, Lindesay J, Parker D (1996) El Niño Southern Oscillation and climatic variability. CSIRO, Australia
- Arroyo MTK, Cavieres L, Marticorena C et al (1995) Convergence in the Mediterranean floras in central Chile and California: insights from comparative biogeography. In: Arroyo MTK, Zedler PH, Fox MD (eds) Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia. Springer-Verlag, New York
- Block M, Richter M (2000) Impacts of heavy rainfalls in El Niño 1997/98 on the vegetation of Sechura Desert in northern Peru (A preliminary report). *Phytocoenologia* 30:491–517
- Brower JE, Zar JH, von Ende CN (1989) Field and laboratory methods for general ecology. WCB McGraw-Hill, Boston
- Collins M (2000) Understanding uncertainties in the response of ENSO to greenhouse warming. *Geophys Res Lett* 27:3509–3512
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive species plants: implications for conservation and restoration. *Annu Rev Ecol Syst* 34:183–211
- Dillon MO, Rundel PW (1990) The botanical response of the Atacama and Peruvian Desert floras to the 1982–1983 El Niño event. In: Glynn PW (ed)

- Global ecological consequences of the 1982–1983 El Niño Southern Oscillation. Elsevier Oceanography Series, Amsterdam
- Figueroa JA, Castro SA, Marquet PA et al (2004) Exotic plant invasions to the mediterranean region of Chile: causes, history and impacts. *Revista Chilena de Historia Natural* 77:465–483
- Fuentes ER, Jaksic FM, Simonetti JA (1983) European rabbits versus native rodents in central Chile: effects on shrub seedlings. *Oecologia* 58:411–414
- Fuentes ER, Otaiza RD, Alliende MC et al (1984) Shrub clumps in the Chilean matorral vegetation: structure and possible maintenance mechanisms. *Oecologia* 62:405–411
- Groves RH (1986) Invasion of Mediterranean ecosystems by weeds. In: Dell B, Hopkins AJM, Lamont BB (eds) *Resilience in Mediterranean-type ecosystems*. Dr. W Junk Publishers, Dordrecht
- Gulmon SL (1977) A comparative study of the grassland of California and Chile. *Flora Bd* 166:261–278
- Gutiérrez JR, Arancio G, Jaksic FM (2000) Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. *J Vege Sci* 11:641–648
- Gutiérrez JR, Meserve PL, Herrera S et al (1997) Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia* 109:398–406
- Hayes GF, Holl KD (2003) Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conserv Biol* 17:1694–1702
- Hobbs RJ, Mooney HA (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* 72:59–68
- Holmgren M (2002) Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. *Biol Invas* 4:25–33
- Holmgren M, Avilés R, Sierralta L et al (2000) Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients, and fire. *J Arid Environ* 44:97–211
- Holmgren M, Scheffer M, Ezcurra E et al (2001) El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol Evol* 16:89–94
- Holmgren M, Stapp P, Dickman CR et al (2006) Extreme climatic events shape arid and semiarid ecosystems. *Front Ecol Environ* 4:87–95
- Jaksic FM, Fuentes ER (1980) Why are native herbs in the Chilean matorral more abundant beneath bushes: microclimate or grazing? *J Ecol* 68:665–669
- Jaksic FM, Fuentes ER (1991) Ecology of a successful invader: the European rabbit in central Chile. In: Groves RH, di Castri F (eds) *Biogeography of Mediterranean invasions*. Cambridge University Press, Cambridge
- López-Cortés F, López D (2004) Antecedentes bioclimáticos del Parque Nacional Bosque Fray Jorge. In: Squeo FA, Gutiérrez JR, Hernández IR (eds) *Historia Natural del Parque Nacional Bosque Fray Jorge*. Ediciones Universidad de La Serena, Chile
- McNaughton SJ (1979) Grassland-herbivore dynamics. In: Sinclair ARE, Norton-Griffith M (eds) *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago
- McPhaden MJ (2004) Evolution of the 2002/03 El Niño. *Bull Am Meteorol Soc* 85:677–695
- Meserve PL, Kelt DA, Milstead WB et al (2003) Thirteen years of shifting top-down and bottom-up control. *BioScience* 53:633–646
- Milchunas DG, Lauenroth WK (1995) Inertia in plant community structure: state changes after cessation of nutrient enrichment stress. *Ecol Appl* 5:452–458
- Montenegro G, Teillier S, Arce P et al (1991) Introduction of plants into the Mediterranean-type climate area of Chile. In: Groves RH, di Castri F (eds) *Biogeography of Mediterranean invasions*. Cambridge University Press, Cambridge
- Noy-Meir I, Gutman M, Kaplan Y (1989) Responses of Mediterranean grasslands plants to grazing and protection. *J Ecol* 77:290–310
- Polis GA, Hurd SD, Jackson CT et al (1997) El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* 78:1884–1897
- Pyke DA, Archer S (1991) Plant–plant interactions affecting plant establishment and persistence on revegetated rangeland. *J Range Manage* 44:550–557
- Rozenzweig ML (1987) Restoration ecology: a tool to study population interactions? In: Jordan WR III, Gilpin ME, Aber JD (eds) *Restoration ecology: a synthetic approach to ecological research*. Cambridge University Press, New York
- Sala OE, Oesterheld M, Leon RJC et al (1986) Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* 67:27–32
- Seabloom EW, Borer ET, Boucher VL et al (2003) Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecol Appl* 13:575–592
- Squeo FA, Arancio G, Gutiérrez JR (2001) *Libro Rojo de la Flora Nativa de la Región de Coquimbo y de los Sitios Prioritarios para su Conservación*. Ediciones de la Universidad de La Serena, La Serena
- Squeo FA, Olivares N, Olivares S et al (1999) Grupos funcionales en arbustos desérticos definidos en base a las fuentes de agua utilizadas. *Gayana Bot* 56:1–15
- Stenseth NC, Mysterud A, Ottersen G et al (2002) Ecological effects of climate fluctuations. *Science* 297:1292–1296
- Tilman D (1993) Species richness of experimental productivity gradients – how important is colonization limitation. *Ecology* 74:2179–2191
- Timmermann A, Oberhuber J, Bacher A et al (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–697
- Trenberth KE, Hoar TJ (1997) El Niño and climate change. *Geophys Res Lett* 24:3057–3060
- Tudhope AW, Chilcott CP, McCulloch MT et al (2001) Variability in the El Niño-Southern Oscillation through a glacial-interglacial cycle. *Science* 291:1511–1517

---

von Ende CN (1993) Repeated measures analysis: growth and other time-dependent measures. In: Scheiner S, Gurevitch J (eds) The design and analysis of ecological experiments. Chapman and Hall, New York

Waser NM, Price MV (1981) Effects of grazing on richness of annual plants in the Sonoran Desert. *Oecologia* 50:407-411

Watt A, Gibson CWD (1988) The effects of sheep grazing on seedling establishment and survival in grassland. *Vegetatio* 78:91-98

Zar JH (1999) Biostatistical analysis. Prentice Hall, New Jersey